Templates for the Organization of Collembolan Communities

by

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The food and habitat are biogenic and of plant and animal origin in terrestrial ecosystems. In terrestrial ecosystems, organic matters are accumulated as plant and soil organic biomass and provide the food and habitat for animal populations. In soil sub-systems, the food-habitat templates are provided mainly by the plant litter such as leaves, branches and fallen logs. The structure and composition of litter are modified through the decomposition processes and provide foods and microhabitats for soil animals. Here, I showed the importance of such food-habitat templates for the organization of soil animal communities by showing the relationships between the templates and collembolan communities in the soil with a Moder humus in a pine forest. Then, the relationships were examined using the field manipulation experiments. Finally, forest ecosystem functions were related to the organization and maintenance of collembolan communities in the soil system. This study is a synthesis of a long term study of collembolan communities in a pine forest soil over a 19 year period.

Introduction

A community is a pattern of individual populations living together in a habitat. So, habitats are the templates for the organization of communities. The dynamic and structural properties of habitats have been related to the life history strategies of organisms such as the r/K selection [MacArthur and Wilson 1967], and the ruderal, competitive and tolerant strategies of plants [Grime 1977]. These habitat properties have been central topics of population and community ecology [Southwood 1977, McCoy and Bell 1991]. But it has not been noticed that the food and habitat are biogenic and of plant and animal origin in terrestrial ecosys-

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tems. In terrestrial ecosystems, organic matters are accumulated as plant and soil organic biomass and provide the food and habitat for animal populations. So, the net primary production of plants provides the template of food and habitat for organisms [Takeda 1992].

In forest ecosystems, less than 10% of the net primary production (NPP) flows into the grazing food chain, which starts from green plants, goes to grazing herbivores and into carnivores [Whittaker 1975]. The majority of NPP is stored in the plant biomass, such as stems, branches and leaves above ground and provides a food-habitat template for the animals of the grazing food chain. Finally, the organic matter source flows into the soil system and provides a food habitat template for the organization of a detritus food chain in the soil. Thus, organic matter produced by plants provides the base of the food habitat templates for the organization of animal communities in the ecosystems.

In soil sub-systems, the food-habitat templates are provided mainly by the plant litter such as leaves, branches and fallen logs. The structure and composition of litter are modified through the decomposition processes and provide foods and microhabitats for soil animals. Thus, the food-habitat templates for soil are maintained dynamically by both processes, i.e., the litter supply and decomposition processes in the soil systems. These template characteristics of forest soils are reflected in the developments of soil organic layers such as the Mull, Moder, and Mor humus forms [Green et al. 1993]. The genesis of the soil organic layers have been related to the roles of soil animals. In the Mull humus form, the macro-invertebrates are dominant. In the Moder or Mor humus forms, the micro-arthropods such as Collembola and Acari are more abundant animal groups [Petersen and Luxton 1982]. Since the beginning of soil ecology, the community organization of soil animals has been a central topic [Agrell 1941, Gisin 1943]. There are some attempts to demonstrate soil animal community patterns in the context of recent community ecology [Usher et al. 1982, Usher 1985, Coleman 1985, Freckman et al. 1986]. Soil communities provide excellent systems for testing hypotheses in current community ecology [Diamond and Case 1986].

Here, I showed the importance of such food-habitat templates for the organization of soil animal communities by showing the relationships between the templates and collembolan communities in the soil with a Moder humus form in a pine forest. Then, the relationships were examined using the field manipulation experiments. Finally, forest ecosystem functions, such as litter fall supply and decomposition processes of organic matter, were related to the organization and maintenance of collembolan communities in the soil system. This study is a synthesis of a long term study of collembolan communities in a pine forest soil over a 19 year period. The details of this study were published in Takeda [1987b].

Study Site and Methods

This study was carried out in a Japanese red pine (*Pinus densiflora* Sieb. et Zucc.) forest mixing with *Chamaecyparis obtusa* Endl. at the Kamigamo Experimental Forest Station of Kyoto University, about 12 km north of the centre of Kyoto City (35°04'N, 135°43'E). Mean monthly temperature ranged from 3.3°C in February to 28°C in August. The mean annual precipitation and evaporation were 1678 mm and 986 mm during the study period. Summer precipitation was high but due to high evaporation caused by high temperatures, the surface layer of organic soil was subjected to drought. The soil profile showed no well-developed structure with no transition zone between the A layer and the B layer. The boundary between the A layer and the B layer is very sharp. The soil organic layer (Ao) of about 3 cm in thickness developed on the A layer of about 1 cm in thickness and consisted of L, F, and H layers. The soil organic layer was of a Moder humus in this study area.

Field Observation on Population and Community Dynamics

A sampling plot of 10 m × 20 m in area chosen in the pine forest was divided into 20 subplots each 2 m × 5 m in area. During the period from July 1971 to June 1982 (except for 1976 and 1977), sampling was done at about monthly intervals. During the period from 1982 to 1990, sampling was done in December. Soil samples consisted of soil cores of each 25 cm^2 in area and 4 cm deep. This sampling depth generally included all the organic layer which contained the vast majority of collembolan populations [Takeda 1978]. The number of soil cores collected was fifteen to twenty-five on each sampling occasion.

Soil arthropods were extracted at a constant temperature of 35°C using a high gradient canister extractor [MacFadyen 1961] which is a standard extraction method for soil microarthropods [Edwards 1991]. The extraction efficiency of this extractor is sufficient for the present study [Takeda 1979b]. The period of extraction was six days. Animals were collected into a solution of saturated picric acid. Identification, counting and measurement were carried out under a binocular microscope with a micrometer eyepiece at 40 × and 400 × magnification.

Field Manipulation of Habitat Templates

Field experiments on the manipulation of the habitat were carried out using the litter bag methods [Crossley and Hoglund 1962]. Freshly fallen litter was collected in the study area using 20 litter traps of each 25 cm × 25 cm in area during the winter period from December to January, 1980, 1981 and 1983 [Takeda 1987a]. The litter collected was used for the litter bag studies. Litter bags measuring 10 cm × 10 cm in area with a mesh size of 1.5 mm were constructed

for the three manipulation experiments.

In the first experiment, three types of litter bags were used to examine the responses of populations and communities to the manipulation of amount of litter. Newly-fallen pine needles were collected in this study area and air-dried at room temperature. Litter bags containing 1, 3, and 9 g pine needles were prepared to this study. Each treatment consisted of ten litter bags. These litter bags were set in the study area divided into 20 subplots each of 1 m × 5 m in area. Within the sub-plots, a 1 m × 1 m area was delimited and then litter bags were set on the forest floor in February 1981, after clearing the newly-fallen litter. The litter bags were collected in February 1982 after exposure for one year.

The second experiment was designed to examine the responses of populations and communities associated with the heterogeneity of habitat conditions. This experiment was carried out from February 1983 to February 1984 in the same study plot as the first experiment. Habitat heterogeneity was manipulated by mixing two different types of litter, i.e., the needle litter of *Pinus densiflora* and the broad leaf litter of *Alnus pendula*. Four types of habitat templates were prepared using litter bags containing different ratios of the two types of litter. Ratios of the litter in the 4 templates were as follows, (1). 3 g of pine needles, (2). 2 g of pine needles plus 1 g of *Alunus*, (3). 1 g of pine needle plus 2 g of *Alunus* and (4). 3 g of *Alunus* litter. In the four templates, the amount of litter was fixed to 3 g per a litter bag each 10 cm × 10 cm in area. A total of 80 litter bags were prepared for this experiment and placed on the forest floor in February 1983. After one year, the litter bags were collected.

Third experiment was designed to follow the successional changes in population and community through the decomposition of litter. Three grams of litter were placed in each litter bags. A total of 300 litter bags were prepared for this experiment and were set on the forest floor in February 1979. They were collected at 3 months intervals during the 3 year period from 1979 to 1982. During the period from 1983 to 1985, litter bags were collected only in February. On each collection date, ten litter bags were collected in the study plot.

Results and Discussion

Habitat Templates of Collembola

Figure 1 shows the micro morphological features of the soil. The soil organic layer (Ao) is a main habitat for the soil microarthropod populations, and shows a stratification reflecting the decomposition processes in the soil. The soil organic layers are the main habitat template for the organization of Collembola communities in this study forest. There was a slight increase in the amount of Ao layer during the period from 1971 to 1981. Then the organic layer was stabilized and remained about 3.5 cm in thickness over the period from 1981 to 1989.

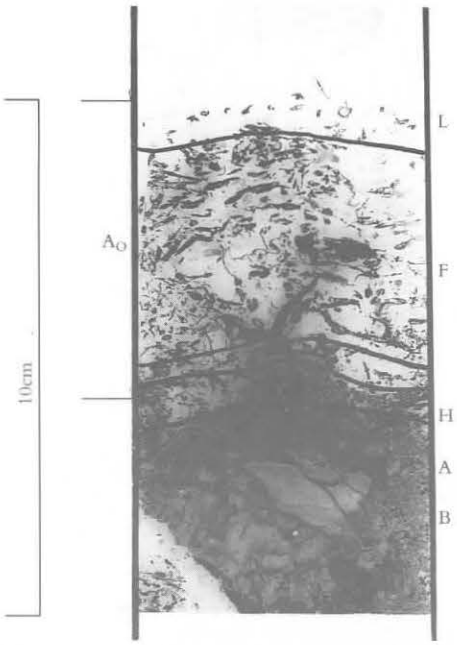

Figure 1. A food-habitat template for the collembolan community. The soil organic layer of the moder humus form in the study forest. Litter accumulated on the forest floor provides the food and habitat for the organization of collembolan community in this forest.

Accumulation of the Ao layer in dry weight was 52 ton/ha. Litter fall was measured over a four year period from 1982 to 1989. In that period, the mean litter fall was 4.6 ton/ha. Litter fall was mainly composed of *Pinus densiflora* and *Chamaecyparis obtusa* needles [Takeda 1987a]. The turn over time of the soil organic layer was about nine years. In this study area, the habitat template of soil animals was thus maintained at an equilibrium state through the litter supply and decomposition processes in the soil.

Temporal Stability of Populations and Communities

Figure 2 shows the relative abundances of soil animal groups in the study forest. Their abundances were comparatively stable over the study period from 1986 to 1990 and resulting in the constant group composition. In the soil animal community, Collembola and Oribatei were the dominant groups during the study period. Mean winter population abundances of collembolan species through a 15 year period from 1971 to 1985 were ranked in their abundance order and shown in Figure 3 together with their standard errors. In this way, the community structure and its stability through a 15 year period are visualized. The dominant ten species accounted for 96.5% of total populations. *Folsomia octoculata*,

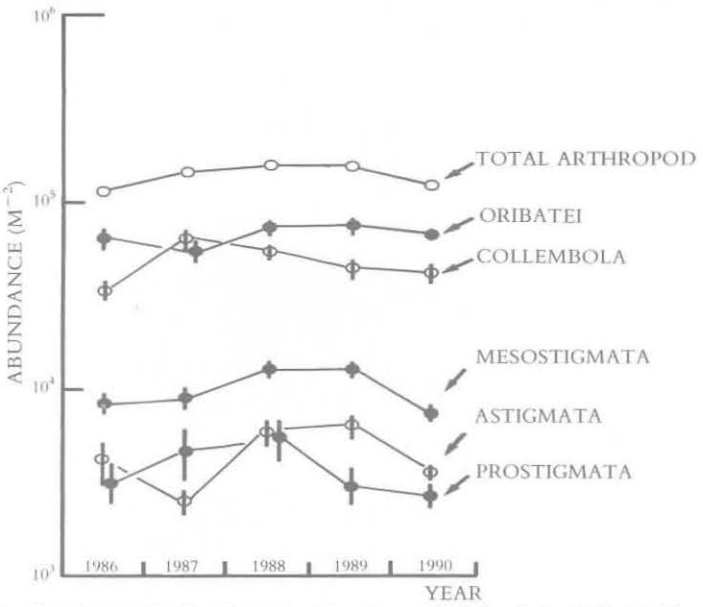

Figure 2. Abundances of soil arthropods. Abundances of Collembola, Oribatei, Mesostigmata, Astigmata, and Prostigmata were shown together with the standard errors. Abundances were based on the winter samples collected in December.

Tullbergia yosii, *Tetracanthella sylvatica* and *Onychiurus decemsetosus* were predominant in the collembolan community and these species were all humus dwellers distributed mainly in the F layer in the soil. The results show a strong dominance of collembolan species in the community structure and composition.

The relative abundance curve together with the standard errors shows that the relative abundance of collembolan species was stable over the 15 year period. The stability of dominant species was expressed by the standard deviation of the log of population abundances over a 15 year period [Connell and Sousa 1983]. The results are shown in Table 1. The collembolan species composition was pre-

Table 1. Annual variability expressed by the standard deviation of the $\log_{10}$ of population abundances.

Species name	Variability
1. *Folsomia octoculata*	0.207
2. *Onychiurus decemsetosus*	0.137
3. *Tomocerus varius*	0.296
4. *Tullbergia yosii*	0.286
5. *Isotoma sensibilis*	0.360
6. *Isotoma carpenteri*	0.261
7. *Folsomina onychiurina*	0.428
8. *Sinella dubiosa*	0.490

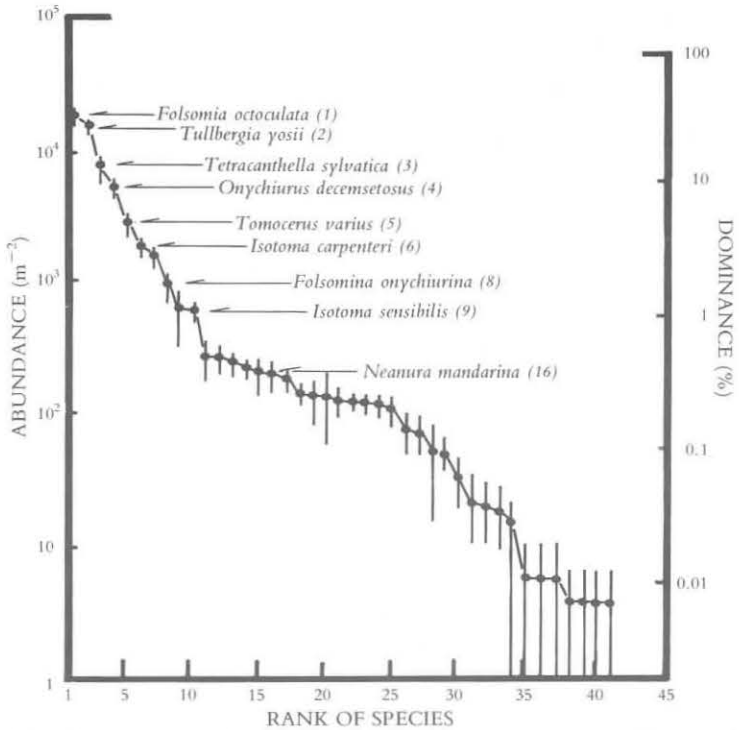

Figure 3. Relative abundance of collembolan species is shown as a percent of the sum of the overall mean abundance for all collembolan species, and a mean abundance per 1 m^2 over a 15 year period. Bars indicate the standard errors. Collembolan species are grouped into the three groups; dominant: above 1%, and rare. 1-0.1%, and very rare group: less than 0.01%.

dictable over the whole study period and was deterministic in the temporal organization. Attributes of this type of deterministic community are its predictability in species composition and community structure over temporal scales, such as season and year. Hence, the community patterns should be explainable by the field observations and manipulation experiments.

Field Observations on the Collembolan Organization

The soil habitat also showed a vertical stratification due to the decomposition processes of litter. The development of the soil organic layer was different from place to place depending on the micro topography within the study plot, and may be reflected in the organization of the collembolan community through the individual habitat selection of collembolan species. Studies of micro-habitat utilization of collembolan species have shown the importance of autoecological responses of collembolan species to the habitat heterogeneity in the vertical and

horizontal scales [Takeda 1978, 1979a, Faber and Joosse 1993].

Collembolan species consisted of the surface, F layer and humus dwellers. The surface-dwelling species included *Tomocerus varius*, *Isotoma sensibilis*, *Homidia subcingula* and *Lepidocyrtus lignorum*. The F layer dwellers were *Folsomia octoculata*, *Onychiurus decemsetousus*, and *Tullbergia yosii* and these species were predominant in the collembolan community. The humus dwellers included *Isotomiella minor*, *Micrisotoma achromata*, and *Folsomina onychiurina*.

The relationships between the depth of the soil organic layer and community parameters, i.e. abundances, diversity and species numbers were examined. There was a significant relationship between the depth of the soil organic layer and the abundances of Collembola ($r = 0.60$, $P < 0.05$). Furthermore, there was a significant relationship between the depth of soil organic layer and number of species ($r = 0.86$, $P < 0.01$). The results suggest that the amount and heterogeneity of the soil organic layer is an important determinant for the structure of the collembolan community in this study plot.

Responses of Collembolan Populations to the Habitat Template

The templates of soil habitat were characterized by two components, i.e., variations in the amount of the soil organic layers, and the structural heterogeneity of the litter. The amount and heterogeneity of the litter determined the types of habitat templates for the collembolan communities. The habitat templates were modified through the litter decomposition processes in soils.

Here I show the results of the three manipulation experiments on the soil habitat templates for the structure and maintenance of the collembolan community in this study area. The first experiment was designed to examine the effects of amount of habitat on the collembolan community structures, the second experiment to explain the effects of habitat heterogeneity on the collembolan community. The third experiment was designed to explain the maintenance mechanisms of the collembolan community through the litter supply and decomposition processes.

Effects of Template Size on Collembolan Community

Responses of Collembola populations to the three levels of amount of habitat are shown in Figure 4. After one year, the abundances of total Collembola populations were 2030, 7110 and 18270 individuals per 1 m^2 for the 1, 3, and 9 g litter bags respectively. The relative abundances observed between the three litter manipulations were not significantly different from the relative abundances calculated from the 1:3:9 ratio of the total individuals collected in the three manipulations ($P < 0.05$).

Abundances of total Collembola were predictable from the amount of habitat. However individual species showed different habitat preferences. The

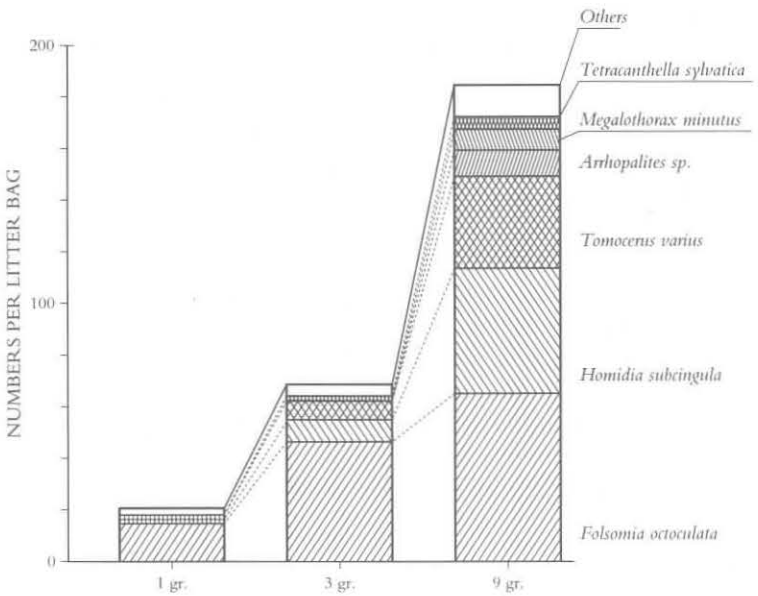

Figure 4. Responses of collembolan species to the three different size templates. Three levels of the amount of habitat were prepared for the colonization of collembolan populations. Each treatment consisted of 10 litter bags. 1 g: 1 g of pine litter in the 100 cm^2 litter bags., 3 g: 3 g of pine litter in the 100 cm^2, and 9 g: 9 g of pine litter in the 100 cm^2

abundances of the surface dwelling species, *Tomocerus varius* and *Homidia subcingula* were higher in the 3 and 9 grams litter bags than in the 1 g litter bags. The predominant species, *Folsomia octoculata*, showed preferences for the 1 and 3 g litter bags. These specific differences in habitat preference may reflect the autoecological responses of individual species to the microhabitat conditions.

Diversity, evenness and species richness were calculated for each manipulation and the results are shown in Table 2. The values of diversity and evenness increased with the increase of amount of habitat. The species richness were higher in the 3 g and 9 g litter bags than in the 1 g litter bags. The results show that the template size represented by the amount of habitat is important determinant

Table 2. Effects of amount of habitat on the community parameters.

Community Parameter	Treatments		
	1 gr.	3 gr.	9 gr.
1. Diversity (H)	1.42	1.90	2.46
2. Evenness (J)	0.40	0.46	0.61
3. Density (m^2)	2030	7110	18270
4. Species	12	17	16

of the community structures, i.e. abundance and diversity of collembolan communities.

Effects of Template Structure on Collembolan Community

Responses of collembolan species and communities to the structural heterogeneity of habitats were studied using the litter bag method. All litter bags contained 3 g of litter, but habitat heterogeneity was different depending on the mixing ratios of two types of litter, i.e. needle (*Pinus densiflora*) and broad leaf (*Alnus pendula*) litter .

The species compositions of the four types of habitat were shown in Figure 5. The most abundant species, *Folsomia octoculata*, showed no habitat preferences in relation to the mixing ratio. Abundances of *Tomocerus varius* and *Tetracanthella sylvatica* increased with the mixing rate of Pine litter, whereas *Homidia subcingula* showed a preference for the *Alunus* litter. As a result of responses of the individual species to habitat heterogeneity, species composition differed between the four habitats. The population abundances of Collembola, diversity,

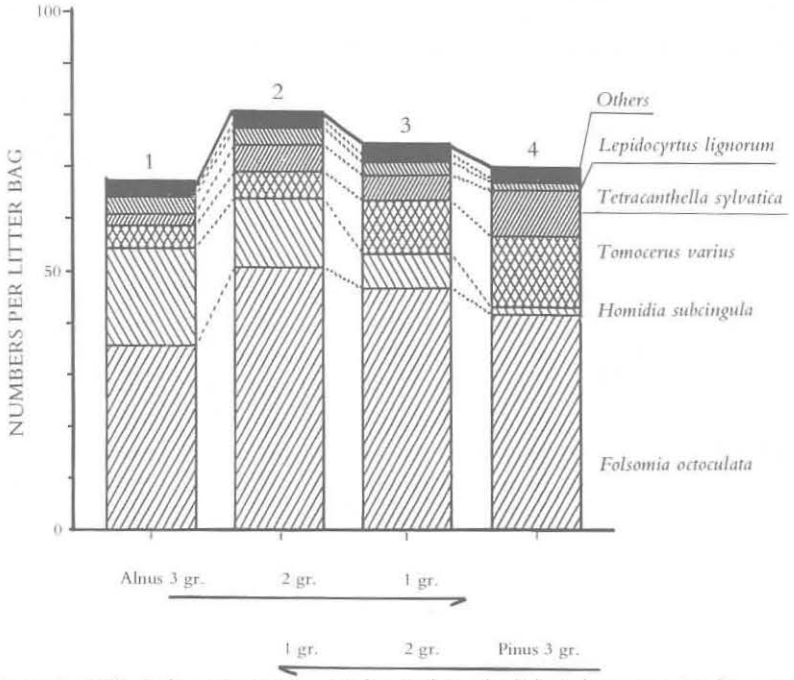

Figure 5. Collembolan communities developed along the habitat heterogeneity. Responses of collembolan populations to the structural heterogeneity of habitats. All litter bags used contained 3g per litter bag (100cm^2). (1): 3 g of *Alunus* litter, (2): 2 g of *Alunus* and 1 g of *Pine* litter, (3): 1 g of *Alnus* and 2 g of *Pine* litter, and (4): 3 g of *Pine* litter .

evenness and species richness were similar between the four habitat [Table 3]. These community parameters were comparable with those in the 3 g litter bags in the first experiment. The results showed that habitat heterogeneity was not related to the community structure of the colonizing species given the same habitat.

Table 3. Effects of habitat heterogeneiry on the community parameters.

Community Parameters	Treatments			
Pine	3 gr	2 gr	1 gr	0 gr
Alunus	0 gr	1 gr	2 gr	3 gr
1. Diversity (H)	1.84	1.98	1.90	1.99
2. Evenness (J)	0.48	0.53	0.49	0.52
3. Density (m^2)	5000	5850	5440	4940
4. Species	14	13	15	14

The results suggest that habitat heterogeneity is not important determinant for the community structure in terms of the abundances, diversity, species richness and evenness, but is important for the species composition through the habitat preferences of individual populations.

Effects of Habitat Modification on the Collembolan Community

The third experiment was designed to follow the successional changes in populations and community through the decomposition of litter. The templates of the food-habitat are modified through the decomposition process by the microbial and soil animal interactions and there have been some studies on successional changes in soil arthropods [e.g. Anderson 1975, Havår and Kjøndar 1981]. Figure 6 shows the species colonizing the litter bags over the 5 year period from February 1979 to February 1984. Thirty-one species colonized the litter bags and they accounted for 85% of the available species pool in this study area. The common species were all encountered in the litter bags community during the 5 year study period.

Figure 6 shows that there was an apparent successional trend in the species composition during litter decomposition. In the early decomposition period when litter bags were in the L layer, the surface dwelling species such as *Tomocerus varius, Isotoma sensibilis, Lepidocyrtus lignorum, Xenella humicola, Tomocerus panctatus,* and *Homidia subcingula* colonized the litter bags. The later colonizing species showed increased abundances with the advance of the decomposition and were comprised of F layer dwellers, such as *Folsomia octoculata, Onychiurus decemsetosus, Tullbergia yosii* and *Megalothrox minimus*. The humus dwelling species, *Microistoma achromata* occurred in the later decomposition stages.

These changes in the species composition were evaluated by the turn-over rates of collembolan species between successive years. The percentage turn-over rates were calculated by the following formula; $(A + B)/C \times 100\%$, where A is

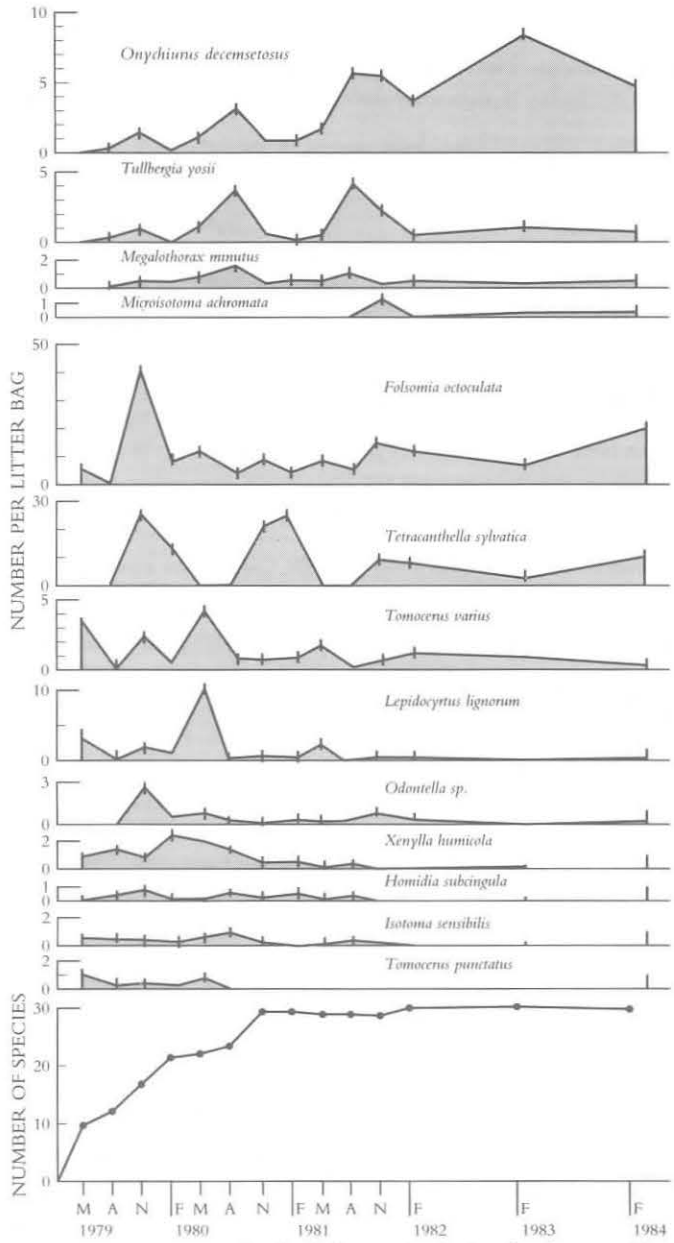

Figure 6. Colonization patterns of collembolan species during the decomposition of litter over a 5 year period. Bars indicate the standard errors intervals.

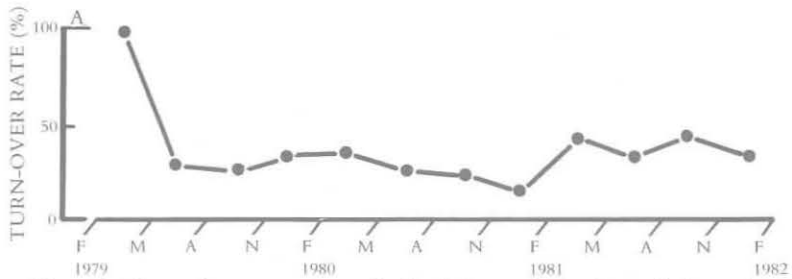

Figure 7. Changes in turn-over rates of collembolan species per 3 months intervals.

the number of immigrant species, B is the number of emigrant species and C is the number of species present at both successive sampling dates. The turn-over rates of species compositions are shown in Figure 7. During the first 3 month intervals, the species turn-over was 100%. Thereafter, the turn-over rates were about 30% and were relatively stable during the study period. The results showed that the decomposition processes of litter accommodated the changes of species composition.

One of the driving factors of the successional trend was the modification of habitats through the decomposition processes of litter. The habitat templates of the collembolan community were composed of the litter of *Pinus* needles. The templates of food-habitat are modified through the decomposition processes in the soil [Verhoef and Brussard 1990]. So, the interactions between microbial and arthropods populations contribut to the modification of templates.

The Functions of Forest Ecosystem Determine the Diversity of Collembolan Community

The communities developed in the litter bags represent a part of the whole communities in the soil. While the species composition of the whole community in the soil was consistent over the 15 year period, the litter bag community showed a successional change in species composition during the decomposition over a 5 year period. The litter bag community was maintained through the immigration and emigration of species into or from the litter bags as shown in Figure 8. The peak of the immigration of species occurred just after the end of litter fall, whereas the emigration showed peaks before the peak of immigration in the first two years during which litter bags were in the L layer.

The emigration and immigration pattern of collembolan species showed the importance of the litter fall, i.e. the renewal of habitat, as the main driving factor in the succession of collembolan communities in the litter bags. After two years, immigration and emigration showed no clear seasonal pattern related to the litter fall, but continuous turn-over of species still resulted from the decomposition of litter.

Litter bag study showed clearly that the collembolan community was

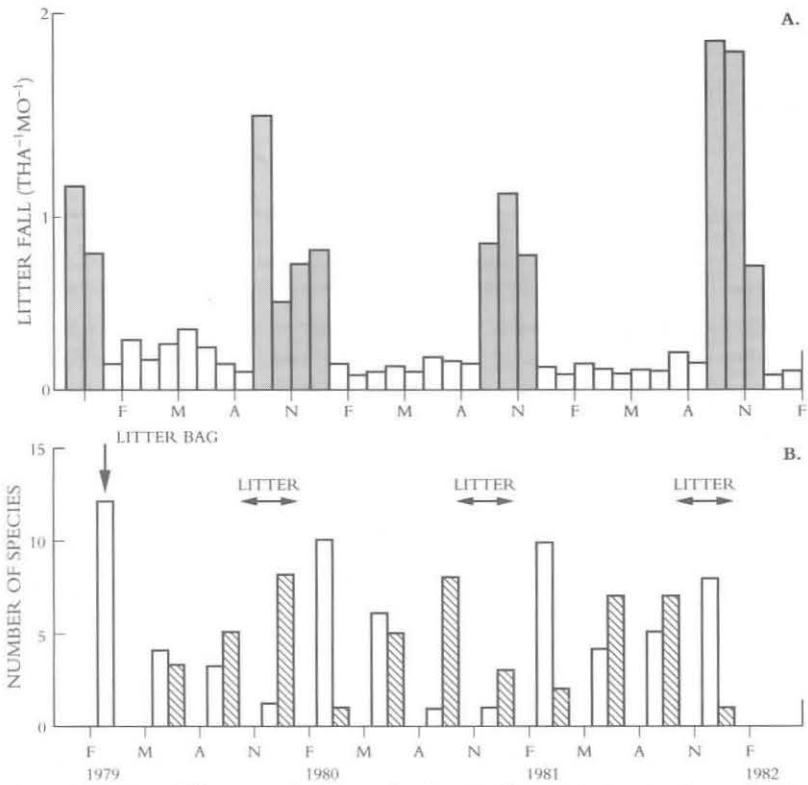

Figure 8. A: litter fall patterns in this study plot, B: Changes in immigration emigration rates of collembolan species per 3 month intervals. In A: Black column indicate the main litter fall in winter period. In B: White column show number of species immigrated into litter bags between the successive sampling occasions. Shaded column show the number of species emigrated from litter bags between the successive sampling occasions. Arrows indicate the main litter fall period in this study forest.

maintained dynamically in an equilibrium state by the responses of individual populations to the renewal and decomposition processes of litter in the soil habitat. The litter supply and decomposition processes are both important functions of forest ecosystems [Kimmins 1987]. Thus these macro-functions of forest ecosystems are contributing to the maintenance of diversity of collembolan communities.

Conclusion

The aims of community ecology is to discover the patterns of populations living together in nature and to explain these patterns by ecological studies.

Community patterns have been explained by the interactions between species through competition and the food web analysis. Here, I showed the importance of food-habitat templates for the organization of collembolan community. In this study, the temporal and spatial organization of collembolan community were demonstrated by population dynamics of collembolan populations and habitat utilization patterns of collembolan populations. In the population dynamics, the equilibrium state of the collembolan community was empirically verified by a long term study of population dynamics of the component species. Then, the community patterns were elucidated by experimental manipulations of the food-habitat templates in a pine forest soil. The collembolan community was highly organized into the food-habitat templates and was maintained at an equilibrium state by the responses of populations to the dynamics of the food-habitat templates. The food-habitat templates were maintained by the litter renewal and decomposition processes, which are both important functions of the forest ecosystems.

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